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AUTHOR(S):

Fujita, Tomohiro

CITATION:

Fujita, Tomohiro. Relative importance of perch and facilitative effects on nucleation in tropical woodland in Malawi. Acta Oecologica 2016, 70: 45-52

ISSUE DATE:

2016-01

URL:

http://hdl.handle.net/2433/203605

Original article

Relative importance of perch and facilitative effects on nucleation in tropical woodland in Malawi☆

Tomohiro Fujita [a, b, *]
tfujita0727@gmail.com
[a]Graduate School of Asian and African Area Studies, Kyoto University, Kyoto 606-8502, Japan
[b]Graduate School of Letters, Kyoto University, Kyoto 606-8501, Japan
[*]Graduate School of Asian and African Area Studies, Kyoto University, Kyoto 606-8502, Japan.
☆Tomohiro Fujita obtained the funding, designed the study, collected data, performed analyses and wrote the manuscript.

Abstract

Individual trees in open vegetation such as woodlands can act as“nuclei” for the colonization of forest tree species, which consequently lead to the formation of forest patches. This phenomenon is known as nucleation. The mechanism of nucleation is generally attributed to two factors: trees provide perches for frugivores that increase seed deposition (perch effect), and tree crowns ameliorate environmental conditions, which improves seedling establishment (facilitative effect). Few studies have attempted to distinguish the relative importance of these two factors. In this study, I separated these two effects in a woodland in northern Malawi. I chose *Ficus natalensis* as a potential nuclei tree because large individuals of this species are commonly located at the center of forest patches within open woodland at the study site. I monitored several environmental variables, seedling survival, seedling composition, and seed rain at three microsites: under*F. natalensis*, under *Brachystegia floribunda* (a dominant woodland species), and in open sites. Both tree species provided similar favorable conditions for the establishment of forest species compared to open sites. Thus, the survival of forest tree seedlings under *F. natalensis* and*B. floribunda* was similar, and substantially higher than seedling survival in open sites. However, communities of naturally occurring seedlings differed significantly between *F. natalensis* and *B. floribunda*. These results indicate that the facilitative effect alone cannot explain the nucleation pattern. I attribute this result to the perch effect of *F.natalensis* because the forest seedling species recorded under *F.natalensis* reportedly have small, brightly colored diaspores, which

are indicative of dispersal by birds. Seed deposition of forest species under*F. natalensis* was significantly higher than that under *B. floribunda* or in open sites. My findings reinforce the idea that trees will lead to nucleation when they enhance seed deposition and have a positive effect on the post-dispersal stage.

Keywords: Facilitation; Ficus; Forest–savanna boundary; Frugivore; Nurse plant; Seed dispersal

1 Introduction

Open vegetation such as grasslands and woodland areas intermingled with closed-canopy forests are common in many tropical regions. Because these tropical forest/open vegetation mosaics cover such large areas, changes to their vegetative structure and composition, and the resulting feedbacks, could have significant implications for biodiversity and the carbon cycle (Mitchard et al., 2009). Although there has been a major loss of forest area caused by logging and other factors, recent studies have also documented the expansion of tropical forests into open vegetation areas in many parts of the world (Puyravaud et al., 2003; Favier et al., 2004; Bowman et al., 2010). Understanding the processes and mechanisms of forest expansion has broad implications for biodiversity conservation and the management of forest/open vegetation mosaics.

The occurrence of individual trees in open vegetation can act as nuclei for the colonization of forest tree species. This process, known as nucleation (Yarranton and Morrison, 1974), can aid colonization of forest tree species, leading to the formation of forest patches. The mechanism of nucleation is generally explained by two different ecological processes (Corbin and Holl, 2012; Zahawi et al., 2013): the perch effect and the facilitative effect. By providing perch sites and fruit, trees in open areas can attract frugivores from nearby forests, and this increases the seed rain of animal-dispersed forest species under their crowns. Additionally, trees in open areas can facilitate forest tree establishment by mitigating stressful environmental conditions, such as high irradiance, high temperatures, and soil water deficits.

Many studies have attempted to verify the mechanisms of nucleation by comparing seedling composition under putative nucleus trees to that in open matrix (e.g., Duarte et al., 2006; Carlucci et al., 2011; Arantes et al., 2014; Fujita and Mizuno, 2015). For instance, Duarte et al. (2006) found more seedlings of forest species established under crowns of *Araucaria angustifolia* than in open matrix in southern

Brazilian grasslands. They attributed this result to the perch effect, given that most seedlings under the crowns had vertebrate-dispersed diaspores. They also suggested that *A. angustifolia* facilitated the establishment of forest species by ameliorating microclimatic conditions such as air humidity and soil water content under the crowns. Other studies have drawn similar conclusions (e.g., Carlucci et al., 2011; Arantes et al., 2014). However, few studies have attempted to separate the relative importance of perch and facilitative effects in the nucleation process (but see Pausas et al., 2006; Albornoz et al., 2013). Nucleation might be generated by either perch or facilitative effect. For instance, nucleation may commence if seeds of forest species are disproportionally deposited under crowns that have neutral effects on post dispersal fate. Alternatively, if the seeds are randomly distributed in space but trees in open areas provide suitable conditions for forest tree species beneath the crowns, nucleation may also occur. Indeed, Vieira et al. (2013) found more seedlings from non-animal dispersed species under *Combretum leprosum*, suggesting that the facilitative effect is the main process driving nucleation in southern Brazilian grasslands. Separating the role of perch and facilitative effects is necessary to fully understand the mechanism of the nucleation.

Trees in the genus *Ficus* (Moraceae) make effective nuclei because their syconia attract many frugivores, and the microhabitat under their dense crowns is suitable for the establishment of forest trees (Slocum and Horvitz, 2000; Slocum, 2001; Schlawin and Zahawi, 2008). In northern Malawi (southeast Africa), circular patches of forest occur within tropical woodland, with large fleshy-fruited trees, especially *Ficus natalensis*, located at their centers (Fujita, 2014). These circular patches are a common feature of nucleated forest patches, rather than fragmented forests (Favier et al., 2004; Duarte et al., 2007). Thus, this region is a suitable field site for testing the nucleation process.

The aim of this study was to elucidate the mechanisms of nucleation by separating the importance of perch and facilitative effects. To address this topic, I compared seedling compositions among three microsites within tropical woodland: under *F. natalensis*, under *Brachystegia floribunda* Benth., and in open microsites. *F. natalensis* and *B. floribunda* have dense crowns that can provide suitable habitat for the establishment of forest tree species. However, *B.floribunda* bears dry pods that are explosively dispersed (Chidumayo and Frost, 1996) and do not attract frugivores, making it unlikely to have a perch effect on seed deposition. If seedling abundance of forest species is higher under *F.natalensis* than under *B. floribunda* or in open microsites, and if the established seedlings are primarily animal-dispersed species, it

suggests the importance of perch effect during nucleation. In contrast, if the abundance and composition of seedlings do not differ under *F. natalensis* and *B. floribunda*, it would suggest that facilitation is the driving force. To address these predictions, I (1) analyzed the environmental conditions in the three microsites, (2) monitored seedling survival of *Syzygium guineense* ssp. *afromontanum* F. White (a forest tree species) in the three microsites for 2.5 years, (3) analyzed the seedling composition in the three microsites, (4) quantified the seed rain of *S. guineense*ssp. *afromontanum* in the three microsites and (5) observed animal visitors at fruiting *F. natalensis* trees.

2 Materials and methods

2.1 Study area

The study was conducted in northern Malawi (southeastern Africa). In southeastern Africa, approximately 2.7 million km^2 of land are covered with tropical woodland called miombo woodland, which consist of leguminous species in three closely related genera: *Brachystegia*, *Julbernardia* and *Isoberlinia*(Fabaceae subfamily Caesalpinioideae; Campbell et al., 1996). This region also contains patchy montane rainforest, which differs from miombo woodland in floristic composition and structure (White et al., 2001). The distributions of miombo woodlands and forest have shifted over wide areas of landscape (Vincens et al., 2003). Ekblom (2008) suggested that climatic conditions after 1850 AD have been favorable for forest expansion.

For these experiments, I selected an area typical to this region in a rural zone managed by the village of Ntchuka (10°58′ S, 34°04’ E) on the north Vipya Plateau in northern Malawi (a map of the study area is available, see Fujita, 2014). Mean annual rainfall on the north Vipya Plateau exceeds 1270 mm, with most rainfall occurring during the wet season between December and April (Chapman, 1970). The bedrock of the Vipya Plateau is composed of undifferentiated basement complex rocks, primarily gneisses (Chapman, 1970). Soil of the study area is a well-drained red and sandy clay loam. The study site is predominantly covered by miombo woodland, although some montane rainforest occurs on mountain crests (>1800 m asl), in valleys, and in several circular forest patches (~10–1800 m^2) on mountainous slopes (1700–1800 m asl). With the exception of montane rainforests, most of the land is burned by humans approximately every 2–3 years during the dry season (September–December). Fires are set to clear footpaths, because overgrown paths are difficult to traverse and pose a risk of hiding snakes. Montane rainforests are typically less flammable due to their dense

canopy that excludes grasses and maintains a more humid understory (Hoffmann et al., 2012a). Therefore, fire is unlikely to penetrate far into the forest. Antelopes such as the common duiker (*Sylvicapra grimmia*) were seen at the study site. Few trees are harvested from this area because it is located far from local villages.

2.2 Study species

F.natalensis is a medium to tall tree species (up to 30 m) distributed in eastern and southern Africa. In the study area, it grows primarily in miombo woodland and is also located at the center of montane rainforest patches. Its syconia (1.1 ± 0.1 × 1.0 ± 0.1 cm, n = 10) change from green to yellowish during ripening. *F.natalensis* has two periods of fruit ripening each year: August–October and January–April. Fruit bats and birds are potential seed dispersers (McCarthy et al., 1998).

Brachystegia floribunda (Fabaceae, Caesalpinioideae) is a medium to tall tree (≤20 m) that is the dominant species in the miombo woodland of northern Malawi, where this study was conducted. The tree produces woody pods (up to 12.5 × 4.0 cm) from October–January; the pods explosively disperse their seeds (Chidumayo and Frost, 1996).

2.3 Data collection

2.3.1 Environmental conditions

To examine whether *F. natalensis* and *B. floribunda* have similar facilitative effects on the establishment of forest tree species, I monitored environmental variables in three microsites: under *F. natalensis*, under *B.floribunda*, and in open microsites. I selected eight *F. natalensis* individuals in miombo woodland that were >50 m from montane rainforest or forest patches. The mean distance between *F. natalensis* trees and forest or forest patches was 169 m (range = 56–307 m). I also selected *B. floribunda* trees and open microsites (3-m radius lacking both trees and canopy cover over 5 cm in dbh) within 50 m of the *F. natalensis* trees. I haphazardly chose eight *B. floribunda* individuals with heights and diameters at breast height (dbh) similar to those of the *F. natalensis*individuals. *F.natalensis* and *B. floribunda* did not exhibit canopy overlap.

I measured the following microhabitat variables: canopy openness, air temperature, relative humidity, soil water content, and the proportion of grass cover. To estimate canopy openness, I took four hemispherical canopy photographs in February 2012 (after the leaves were fully expanded) at each microsite at a height of 1 m above the ground using a fish-eye lens (Raynox DCR-CF; Yoshida Industry, Tokyo, Japan). The pictures were taken at the midpoint of the crown radius in each cardinal direction

from the trunk. At the open microsite, the pictures were taken in each cardinal direction at 1 m from the center of the plot. I then used gap light analyzer software (Frazer et al., 1999) to calculate canopy openness. The overall canopy openness at each microsite was calculated as the mean of the four values. Air temperature and relative humidity were measured every 15 min over three days using a data logger (Ondotori RH TR72U, T and D, Matsumoto, Japan) placed 1 m from the trunk, or in the center of the open microsite. The measurements were made during the dry season (September 2012). Soil water content was measured at 12-cm depth using time domain reflectometry TDR probes (Hydrosense; Campbell Scientific, Townsville, Australia) at the same location where the canopy photographs were taken. The overall soil water content at each microsite was calculated as the mean of the four values. The measurements were made during the dry season (September 2012) and the rainy season (March 2013). In September 2012 before fires occurred, I visually estimated the proportion of grass cover in four 1 × 1-m quadrats (same locations as the canopy photographs), and calculated the grass cover at each site as the mean of these four quadrats.

2.3.2 Seedling survival of a forest species

To examine the facilitative effect of trees on the establishment of forest tree species, I monitored seedling survival of *S. guineense* ssp. *afromontanum* in the three microsites. *Syzygium guineense* ssp. *afromontanum* is endemic to montane rainforest and is a common species in montane rainforests on the Vipya Plateau (White et al., 2001). This species is a medium to tall tree (up to 30 m) that bears purple berries from January to March, with a mean fruit size of 1.6 × 1.4 cm (n = 6). In January 2012, I planted *S. guineense* ssp. *afromontanum* seeds in a nursery. Four weeks after they developed their first true leaves, I transplanted the seedlings into the three field microsites. Under each tree, and in each open microsite, I planted 16 seedlings, separated by 50 cm in a 4 × 4 grid (384 seedlings total). Seedlings were watered immediately after transplanting, but no additional treatments were applied. Initial survival was determined 1 week after planting and seedlings that had died due to transplant shock were replaced. The seedling survival was then monitored at approximately 1, 6, 7, 10, 19 and 31 months following planting.

2.3.3 Seedling composition

In August 2011, prior to the fire season, I measured seedling composition using four 2 × 5-m quadrats placed in the four cardinal directions around each tree trunk, or around the center of the plot in the open microsites. I counted all seedlings (0.2–1 m high) in each quadrat and pooled these data for each plot. Plant specimens were

identified at the National Herbarium and Botanical Gardens of Malawi. I then determined the preferred habitat of each species from the literature (Friis, 1992; White et al., 2001).

2.3.4 Seed rain of Syzygium guineense ssp. afromontanum

I quantified seed rain of *S. guineense* ssp. *afromontanum* from January to March 2012 using seed traps. The traps were 70 × 70 cm of fine-mesh net secured to the ground, with 5-cm-high sides to prevent collected seed from washing away. Three seed traps were placed 1 m from the base of each trunk or 1 m from the center of the open microsites, for a total of 72 seed traps across all plots. The direction of the first quadrat was determined randomly, and the others were placed at 120° and 240° from the first. Each microsite was visited twice per week, and seeds were collected and counted. Seeds from the three traps in a plot were combined for analysis.

2.3.5 Tree observations

Focal observations of four fruiting *F. natalensis* trees in miombo woodlands were carried out from January to March 2011 to estimate the potential dispersers of forest tree species into miombo woodlands. Observations were conducted in three time blocks: 05h30–08h30, 08h30–12h30 and 12h30–15h30. Each tree was observed twice for each time block, one time block per day, and not on successive days. The total observation time for all four trees was 80 h. Each tree was observed from a distance of ~ 20 m using binoculars. For all animal visitors, I recorded the duration of their stay in the tree and their behavior (i.e., whether the animal consumed fruit, fed on arthropods, or just perched on the tree). I classified a behavior as “feeding” when an animal fed on syconia or insects that were visible to the observer. When the animal under observation fed on neither syconia nor insects but perched in the tree, I classified the behavior as“perch”. When two or more individuals of the same species were present within the branch structure of a single tree, I was unable to accurately collect data on all of them. Therefore, I collected data for only one focal individual. Bird and animal species were identified with reference to Kingdon (1974), Fry and Keith (1988), Fry et al. (1988), Keith et al. (1992), Urban et al. (1997), Fry et al. (2004) andDowsett-Lemaire and Dowsett (2006). Based on these sources, I classified each bird and animal species into forest, forest/woodland or woodland species.

2.4 Data analysis

Statistical analyses were conducted using R software ver. 2.14.0 (R Development Core Team; http://www.r-project.org/). Environmental variables were tested for normality (Kolmogorov–Smirnov's test) and homogeneity of variances

(Bartlett's test) prior to statistical analysis. When the data were normal and homoscedastistic, I used a one-way ANOVA followed by Tukey's multiple comparison test (when appropriate) to detect significant differences in the environmental variables among microsites. If the data did not fit the assumptions of inferential parametric statistics, I used the non-parametric Kruskal–Wallis test followed by the Steel–Dwass multiple comparisons test.

The final percent survival of *S. guineense* ssp. *afromontanum* was analyzed using GLM with a binomial log-link function. Tukey's multiple comparison tests were used to detect differences in seedling survival among microsites. The tests were conducted with the glht function in the R multicomp package.

Non-metric multi-dimensional scaling (NMDS) analyses, based on the Bray–Curtis dissimilarity index, were performed to visualize differences in seedling composition among microsites. Furthermore, to investigate whether differences in species composition among microsites were significant, I performed a PERMANOVA using the metaMDS function in the R vegan package.

The species that were typical of the different microsites were determined using the indicator species analysis (Dufrêne and Legendre, 1997) available in the labdsv package of R. This approach calculates an index (Indval) that clearly measures the fidelity of a taxon to a specific range of different habitat types. These indices were tested for statistical significance ($P \leq 0.05$) against random expectations using a Monte Carlo permutation with 1000 replicates.

The numbers of forest species seedlings and the seed rain counts for *S.guineense* ssp. *afromontanum* were discrete variables(i.e., not continuous). These data did not fit the assumption of normality and were therefore analyzed using the nonparametric Kruskal–Wallis test followed by the Steel–Dwass multiple comparisons test to detect significant differences among microsites.

3 Results

3.1 Environmental characterization of the microsites

Although the soil water content did not vary significantly among the microsites, other variables did (Table 1). Canopy openness, mean air temperature and the proportion of grass cover were significantly lower under *F. natalensis* and under *B. floribunda* than in open sites. However, the values for these variables under *F. natalensis* were not significantly different from those under *B.floribunda*. The

air humidity under *F. natalensis* and under *B. floribunda* were significantly higher than those in open sites, but did not differ significantly from one another.

Table 1 Environmental conditions measured among three microsites (means ± SE) in a miombo woodland in northern Malawi.

Dependent variables	Under *Ficus natalensis*	Under *Brachystegia floribunda*	Open
Canopy openness (%)	11.3 ± 1.0a	16.3 ± 2.1a	54.8 ± 3.4b
Ta (°C)	21.6 ± 0.6a	21.6 ± 0.7a	24.8 ± 1.2b
RH (%)	50.4 ± 1.8a	49.8 ± 2.6a	41.4 ± 2.4b
Grass cover (%)	19.5 ± 1.9a	35.0 ± 6.2a	58.8 ± 3.3b
SWC (rainy season) (%)	29.6 ± 1.4	30.4 ± 1.5	30.6 ± 1.3
SWC (dry season) (%)	3.3 ± 0.5	3.0 ± 0.6	2.9 ± 0.5

See the text for microsite definitions. Variables: Ta, mean air temperature; RH, relative humidity; SWC, soil water content. Summary statistics of tests for significant differences in the dependent variables among the independent variables: canopy openness, $x2 = 16.81$, $df = 2$, $p < 0.001$; Ta, $F = 25.32$, $df = 2$, $p < 0.0001$; RH, $F = 37.15$, $df = 2$, $p < 0.0001$; grass cover, $x2 = 14.95$, $df = 2$, $p < 0.001$; SWC (rainy season), $F = 0.14$, $df = 2$, $p = 0.87$; SWC (dry season), $F = 0.20$, $df = 2$, $p = 0.82$. Different lower case letters following numerical values indicate significant pairwise differences ($\alpha = 0.05$, Tukey's test or the Steel–Dwass test) in the same row.

3.2 Seedling survival

Of the *S. guineense* ssp. *afromontanum* seedlings initially planted, 41.7% survived until the end of the experiment. Seedling survival at the end of the experiment was significantly affected by microsite (Fig. 1). Seedling survivals under *F. natalensis* and under *B. floribunda* were significantly higher than the survival in open sites. However, the value under *F. natalensis* was not significantly different from those under *B. floribunda*. The cumulative survival of seedlings under *F. natalensis* and *B. floribunda* was sixfold higher than in open sites.

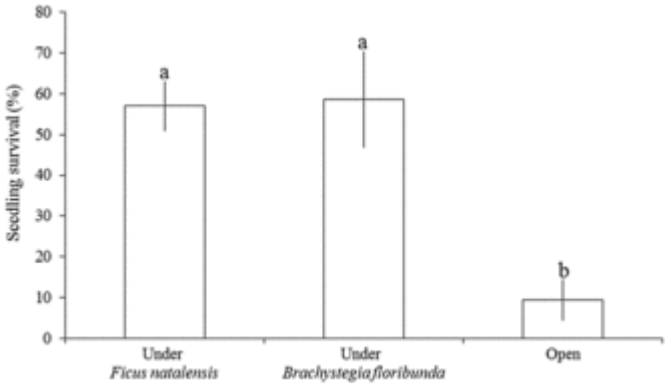

Fig. 1 Mean seedling survival of *Syzygium guineense* ssp. *afromontanum* (±1 SE) in three microsite environments in a miombo woodland in northern Malawi. Seedling survival (n = 384) was measured from February 2012 to August 2014. Means followed by the same letter are not significantly different ($P > 0.05$) among microsites based on Tukey's post hoc tests.

3.3 Composition of seedling communities

In total, I found 401 seedlings from 39 tree species. The NMDS (stress = 0.12) showed that seedling composition differed among the three microsites (Fig. 2). Seedling composition under *F. natalensis* differed significantly from the seedling composition under *B. floribunda* (PERMANOVA, pseudo-$F = 3.24$, $P < 0.01$) and in open sites (PERMANOVA, pseudo-$F = 5.48$, $P < 0.01$). In contrast, there was no statistical difference in the seedling communities under*B. floribunda* and those in open sites (PERMANOVA, pseudo-$F = 1.14$, $P = 0.34$). Of the seedlings counted, 152 individuals (38%) from 18 species were characterized as forest or forest-related taxa (forest/woodland species; Table 2). Most of these seedlings (93%) were found under *F. natalensis*. The seedling numbers of forest and forest-related species were significantly greater under *F.natalensis* than under *B. floribunda* (Steel–Dwass multiple comparisons test, $t = 3.34$, $P < 0.01$) or at open sites (Steel–Dwass multiple comparisons test, $t = 3.59$, $P < 0.01$). Diaspores of these species possessed characteristics associated with vertebrate dispersal (Table 2). Six “indicator species” were identified for *F.natalensis* sites: *Mystroxylon aethiopicum* (Thunb.) Loes. (Celastraceae),*Diospyros whyteana* (Hiern) F. White (Ebenaceae), *Apodytes dimidiata* E Mey. (Icacinaceae), *S. guineense* ssp. *afromontanum*, *Prunus africana* (Hook. f.) Kalkman (Rosaceae), and *Rhus longipes* Engl. (Anacardiaceae). All of these, with the exception of *R. longipes*, are forest or forest-related species (Table 2). In contrast, I was unable to identify any specific indicator species under *B.floribunda* or for open sites.

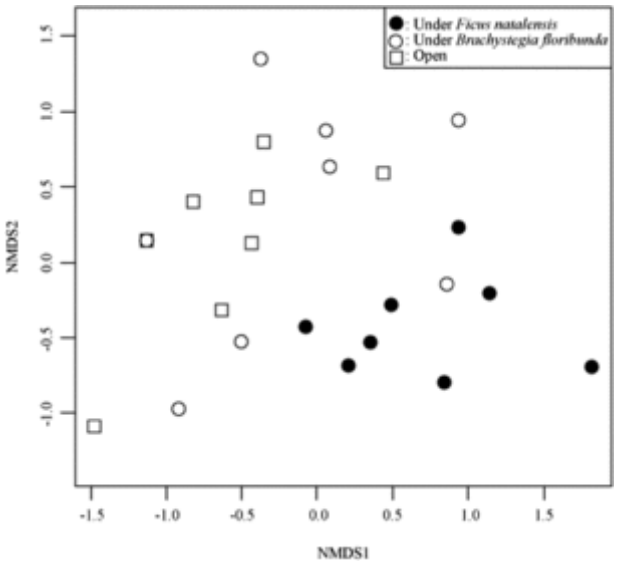

Fig. 2 Non-metric multidimensional scaling ordination of seedling compositions for three microsite classes in a miombo woodland in northern Malawi. Dissimilarities between sites were calculated using the Bray–Curtis distance based on counts at each site.

Table 2 List of woody plant seedling at three microsites in northern Malawi.

Species name	Family	Fruit size (mm)	Fruit color	Mode of seed dispersal	Habitat	No. of seedlings		
						Fn	*Bf*	Open
***Rhus longipes*Engl.**[a]	Anacardiaceae	6 × 5	brown	animal	woodland	22	1	0
*Ozoroa insignis*ssp. *reticulata*(Baker f.) J.B. Gillett[b]	Anacardiaceae	unknown	black	animal	woodland	0	0	1
*Cussonia arborea*Hochst. ex A. Rich.[a]	Araliaceae	5 in dia.	purple	animal	woodland	5	4	1
*Cussonia spicata*Thunb.[a]	Araliaceae	7 × 7	purple	animal	for./woodl.	13	0	0
Schefflera umbellifera(Sond.) Baill.[a]	Araliaceae	3 in dia.	red	animal	forest	3	0	0
*Tecoma nyassae*Oliv.[b]	Bignoniaceae	unknown	unknown	unknown	woodland	0	1	0
*Brachystegia floribunda*Benth.[a]	Caesalpinioideae	–	–	explosive	woodland	17	21	40
Brachystegia boehmii Taub.[a]	Caesalpinioideae	–	–	explosive	woodland	0	3	10
***Mystroxylon aethiopicum*(Thunb.) Loes.**[c]	Celastraceae	16 × 15	red	animal	for./woodl.	14	0	0
*Parinari curatellifolia*Planch. ex Benth.[a]	Chrysobalanaceae	50 × 20	yellow	animal	woodland	0	0	3
Monotes africanus A. DC.[a]	Dipterocarpaceae	–	–	wind	woodland	0	0	8

Species name	Family	Fruit size (mm)	Fruit color	Mode of seed dispersal	Habitat	No. of seedlings		
						Fn	*Bf*	Open
***Diospyros whyteana*(Hiern) F.White**[c]	Ebenaceae	20 × 20	red	animal	forest	14	1	0
*Euclea racemosa*ssp. *schimperi* (A. DC.) F. White[c]	Ebenaceae	10 in dia.	red	animal	for./woodl.	2	0	0
Erica benguelensis(Welw. ex Engl.) E.G.H. Oliv.[a]	Ericaceae	unknown	unknown	unknown	woodland	0	0	5
*Croton macrostachyus*Hochst. ex Delile[d]	Euphorbiaceae	5 in dia.	green	animal	for./woodl.	3	0	0
*Aeschynomene schliebenii*Harms[a]	Fabaceae	–	–	unknown	woodland	0	13	13
Erythrina abyssinica Lam.[a]	Fabaceae	–	–	explosive	woodland	2	0	0
Scolopia sp.	Flacourtiaceae	unknown	unknown	unknown	unknown	2	0	0
*Psorospermum febrifugum*Spach[a]	Hypericaceae	7 × 7	red	animal	woodland	1	0	2
***Apodytes dimidiata* E.Mey. ex Arn.**[c]	Icacinaceae	10 in dia.	black	animal	forest	16	0	0
*Grewia stolzii*Ulbr.[c]	Malvaceae	30 in dia.	unknown	animal	forest	0	1	0
Dissotis johnstoniana var.*johnstoniana*Benth.[b]	Melastomataceae	unknown	unknown	unknown	woodland	22	1	0
*Trichilia emetica*Vahl[e]	Meliaceae	20 × 10	red	animal	for./woodl.	4	0	0

Species name	Family	Fruit size (mm)	Fruit color	Mode of seed dispersal	Habitat	No. of seedlings		
						Fn	*Bf*	Open
Bersama abyssinica var.*engleriana*(Gürke) F. White[a]	Melianthaceae	10 × 8	red	animal	for./woodl.	1	1	0
Rapanea melanophloeos(L.) Mez[d]	Myrsinaceae	8 × 8	purple	animal	for./woodl.	2	0	0
Syzygium guineense* ssp.*afromontanum* *F*. *White[c]	Myrtaceae	16 × 14	purple	animal	forest	36	2	0
*Ochna schweinfurthiana*F. Hoffm.[a]	Ochnaceae	7 × 6	black	animal	woodland	0	1	0
Schrebera alata(Hochst.) Welw.[c]	Oleaceae	–	–	explosive	forest	3	0	0
*Uapaca kirkiana*Müll. Arg.[a]	Phyllanthaceae	25 × 24	yellow	animal	woodland	0	10	5
Bridelia bridelifolia (Pax) Fedde[a]	Phyllanthaceae	8 × 7	black	animal	for./woodl.	6	5	0
*Faurea speciousa*Welw.[a]	Proteaceae	–	–	wind	woodland	3	3	5
*Protea angolensis*Welw.[a]	Proteaceae	–	–	wind	woodland	0	0	6
Protea petiolaris(Hiern) Baker & C.H. Wright[a]	Proteaceae	–	–	wind	woodland	0	0	1
***Prunus africana*(Hook. f.)Kalkman**[c]	Rosaceae	10 × 7	brown	animal	forest	13	0	0
Oxyanthus	Rubiaceae	30 in dia.	yellow	animal	forest	2	0	0

Species name	Family	Fruit size (mm)	Fruit color	Mode of seed dispersal	Habitat	No. of seedlings		
						Fn	*Bf*	Open
speciosus spp.*stenocarpus* (K. Schum.) Bridson[c]								
Psydrax schimperiana(A.Rich.) Bridson[c]	Rubiaceae	10 in dia.	black	animal	forest	4	0	0
*Allophylus chaunostachys*Gilg[c]	Sapindaceae	6 in dia.	red	animal	for./woodl.	6	0	0
unknown 1						2	12	0
unknown 2						2	1	0

Fn, under *Ficus natalensis*; Bf, under *Brachystegia floribunda*; Open, open microsites for., forest; woodl., woodland; dia., diameter.

Significant indicator species for *F. natalensis* sites are in bold type.

[a]Coutes Palgrave (2002).

[b]Flora Zambesiaca.

[c]White et al., 2001.

[d]Friis (1992).

[e]Van wyk and Van Wyk (1997).

3.4 Seed rain

Sixty-seven seeds of *S. guineense* ssp. *afromontanum* were found. The rate of seed deposition differed significantly among microsites (Fig. 3). Most dispersed seeds (85%) were found under *F. natalensis*. The number of dispersed seeds was significantly higher under *F. natalensis* than in the other two microsites. Dispersed seeds of *S. guineense* ssp. *afromontanum* were found under all eight *F.natalensis* individuals.

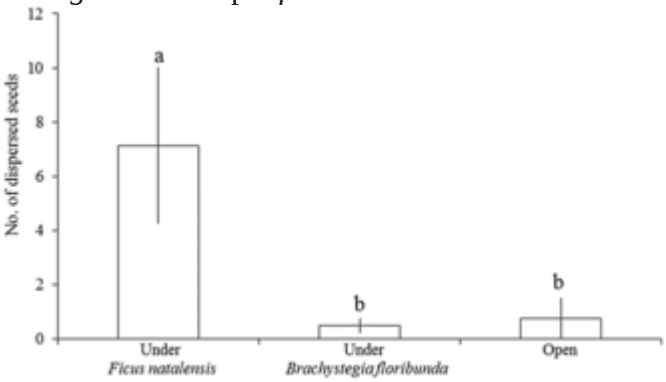

Fig. 3 Mean number (±SE) of *Syzygium guineense* ssp. *afromontanum* seeds dispersed at three microsites in a miombo woodland in northern Malawi. The seed rain was monitored from January to March 2012. Means with the same lower case letters are not significantly different ($P > 0.05$; Tukey's post hoc test) among microsites.

3.5 Animal visits to F. natalensis

During 80 h of focal observations, I observed 21 bird and 1 mammal species at *F. natalensis*, of which 10 species were frugivores (Table A.1). Seven of the frugivore species were species that primarily use forest habitat. These accounted for 52% of all visiting animals. The two most abundant forest-related frugivores were sun squirrels (0.6 counts/h) and Schalow's turacos (0.4 counts/h).

Table A.1 Animal visiting fruiting *Ficus natalensis*trees in a miombo woodland in northern Malawi, their body masses, diets, habitats, observed behaviors, numbers of visits (n), and visit durations (total and median).

Name		Body mass (g)	Diet	Habitat	Observed behavior	Visits (n)	Total duration (min)	Median duration (min)
Birds								
Columba arquatrix(Temminck)[a]	African olive pigeon	300–480	Frugivore	Forest	Perching	3	13.6	4.2
Tauraco schalowi(Reichenow)[b]	Schalow's turaco	210–270	Frugivore	Forest/Woodland	Foraging for syconium	29	121.1	3.7
Treron calva(Temminck)[a]	Afrcan green pigeon	210–250	Frugivore	Woodland	Foraging for syconium	2	5.5	2.8
Onychognathus morio(Linnaeus)[c]	Red-winged starling	120–155	Frugivore	Woodland	Perching	1	5.4	5.4
*Malaconotus blanchoti*Stephens[c]	Grey-headed bush-shrike	65–95	Non-frugivore	Woodland	Foraging for insect	2	1.1	0.6
Turdus libonyana(Smith)[d]	Kurrichane thrush	50–70	Frugivore	Woodland	Foraging for syconium	22	64.7	1.4
Pycnonotus tricolor(Hartlaub)[b]	Dark-capped bulbul	30–48	Frugivore	Forest/Woodland	Foraging for	3	4.7	1.6

Name		Body mass (g)	Diet	Habitat	Observed behavior	Visits (n)	Total duration (min)	Median duration (min)
					syconium			
Chrysococcyx caprius(Boddaert)[b]	Diderick cuckoo	22–42	Non-frugivore	Woodland	Foraging for insect	1	0.3	0.3
Muscicapa caerulescens(Hartlaub)[a]	Ashy flycatcher	15–17	Frugivore	Forest/Woodland	Foraging for insect	12	13.2	0.7
Chalcomitra amethystina(Shaw)[c]	Amethyst sunbird	11–19	Non-frugivore	Forest/Woodland	Foraging for syconium	1	7.1	7.1
Terpsiphone viridis (Statius Müller)[e]	African paradise-flycatcher	11–17	Non-frugivore	Forest/Woodland	Foraging for insect	3	1.1	0.4
Ficedula albicollis(Temminck)[e]	Collared flycatcher	10–14	Non-frugivore	Woodland	Foraging for insect	47	53.8	0.9
Lagonosticta rhodopareia(Heuglin)[f]	Jameson's firefinch	8–13	Non-frugivore	Woodland	Perching	1	0.5	0.5
Zosterops senegalensis(Bonaparte)[c]	African yellow white-eye	8–11	Frugivore	Forest/Woodland	Foraging for syconium	1	0.4	0.4
*Cinnyris manoensis*Reichenow[c]	Miombo double-collared sunbird	8–11	Non-frugivore	Forest/Woodland	Perching	1	1.7	1.7

Name		Body mass (g)	Diet	Habitat	Observed behavior	Visits (n)	Total duration (min)	Median duration (min)
Phylloscopus trochilus(Linnaeus)[a]	Willow warbler	7–12	Non-frugivore	Forest/Woodland	Perching	1	1.2	1.2
Hedydipna collaris(Vieillot)[c]	Collared sunbird	6–11	Frugivore	Forest/Woodland	Perching	1	0.2	0.2
Cinnyris venustus(Shaw)[c]	Variable sunbird	6–10	Non-frugivore	Forest/Woodland	Perching	1	1.5	1.5
unidentified bird 1					Foraging for syconium	4	5.5	1.3
unidentified bird 2					Foraging for syconium	1	3.1	3.1
unidentified bird 3					Perching	1	1.4	1.4
Mammal								
Heliosciurus mutabilis(Peters)[g]	Sun squirrel	400	Frugivore	Forest/Woodland	Foraging for syconium	48	850.2	14.7

[a]Fry et al. (1988).

[b]Dowsett-Lemaire and Dowsett (2006).

[c]Fry and Keith (1988).

[d]Keith et al. (1992).

[e]Urban et al. (1997).

[f]Fry et al. (2004).

[g]Kingdon (1974).

4 Discussion

4.1 *Ficus natalensis* and *B*

floribunda provided conditions for the establishment of forest species that were similar to one another and better than those in the open sites (Table 1). Indeed, the survival of *S. guineense* ssp. *afromontanum* seedlings under *F.natalensis* and *B. floribunda* was similar, and seedling survival under these trees was significantly higher than that in open sites (Fig. 1). In contrast, the composition of naturally recruiting seedling communities differed significantly under *F. natalensis* and *B. floribunda* (Fig. 2). I attribute this result to the perch effect provided by *F. natalensis*, which promoted seed deposition by frugivorous birds. Most seedlings under *F. natalensis* are reported to have small, brightly colored diaspores, suggesting bird dispersal (Table 2). Seed deposition of *S.guineense* ssp. *afromontanum* under *F. natalensis* was much higher compared to*B. floribunda* or open sites (Fig. 3). Furthermore, forest-related frugivores were observed frequently visiting fruiting *F. natalensis* (Table A1). These results support the importance of the perch effect provided by *F. natalensis* for nucleation.

Few studies have demonstrated the role of tree perches in the nucleation process separately from the role of the facilitative effect. Pausas et al. (2006) identified the importance of the perch effect on nucleation in Mediterranean abandoned fields when making a comparison of seedling distributions between fleshy fruit species and non-fleshy fruit species. The seedlings of fleshy fruit species were positively associated with shrubs, while seedlings of non-fleshy fruit species were randomly distributed (Pausas et al., 2006). My quantitative comparisons of the establishment of forest tree species under fleshy fruit versus non-fleshy fruit trees demonstrate the importance of species-specific interactions in seed deposition during the early stages of nucleation in sparse open woodlands of southeastern Africa.

Overlapping fruiting seasons among plants that share seed dispersal agents can enhance the seed dispersal of exotic plant species during the invasive process (Battaglia et al., 2009; White and Vivian-Smith, 2011) and may promote the process of mistletoe infection of host trees (Carlo and Aukema, 2005). White and Vivian-Smith (2011), for example, demonstrated that the seed rain of exotic species was substantially higher under synchronously fruiting crowns than under non-fruiting crowns. A similar mechanism may operate during the spread of forests into sparse open vegetation. Although *Ficus* trees are generally known to exhibit inter-tree asynchrony in syconia

production (Shanahan et al., 2001), *F.natalensis* has two peaks of ripening each year (in August–October and in January–April; Dowsett-Lemaire, 1985). These peaks of syconia maturation partially overlap with fruit set in montane rainforests in this region (Dowsett-Lemaire, 1985). Thus, the timing of fruit ripening in *F. natalensis* may drive the observed pattern of forest tree establishment under *F. natalensis* in miombo woodland. Future studies should determine whether the timing of fruit maturation in nuclei trees promotes the nucleation process in sparse open vegetation.

Individual animal species are likely to vary in their contribution to the seed deposition of animal-dispersed forest species under *F. natalensis*, depending on their diet, handling behavior, and habitat dependency (Kitamura et al., 2002; Lehouck et al., 2009). Among the animals observed here, Schalow's turaco is likely to be an important disperser of forest species in miombo woodland because it consumes a wide range of fruits in montane rainforests and can swallow fruits up to 30 mm in diameter (Dowsett-Lemaire, 1988). Although Schalow's turacos prefer forest habitats (Fry and Keith, 1988), they are not biome-restricted (Mills et al., 2008). In fact, Schalow's turacos were frequently observed visiting fruiting*F. natalensis* in miombo woodland (Table A1). Other forest-related frugivores, such as African green pigeons and dark-capped bulbuls, recorded during observations may also contribute to forest seed transport, especially for small-seeded species.

Although I have highlighted the importance of the perch effect so far, my results do not reject the importance of a facilitative effect as a driver of nucleation. Seedling survival of *S. guineense* ssp. *afromontanum* in open sites was nearly sixfold lower than under *F. natalensis* (Fig. 1). This result indicates that seedlings of forest species cannot persist without the facilitative effect of nearby trees in miombo woodland.

Shade provided by tree crowns may protect seedlings from desiccation (Gomez et al., 2005). The lower air temperature and solar radiation, and higher air humidity measured under *F. natalensis* crowns in comparison with open areas can reduce leaf temperature and transpiration losses, creating a more favorable water balance for forest tree seedlings, even in the absence of microsite differences in soil water content (as observed by Gomez et al., 2005). In addition, because grass cover is lower under *F. natalensis* compared to open sites, seedling survival can be facilitated by reduced competition with grass and the suppressed occurrence of fire (Shararn et al., 2009; Hoffmann et al., 2012b; Salazar et al., 2012). This array of modifications under the *F. natalensis* crown could result in higher establishment of forest species under the stressful environmental conditions found in miombo woodland.

Syzygium guineense ssp. *afromontanum* seeding survival was also enhanced under *B. floribunda* (Fig. 1), where environmental conditions are ameliorated in the same way as under *F. natalensis* (Table 1). However, I found little seedling establishment of forest species under *B. floribunda* (Table 2), likely because of seed limitation (i.e., seeds did not reach suitable habitats). The seed rain monitoring measurements detected few *S. guineense* ssp. *afromontanum*seed arrivals under *B. floribunda* canopy (Fig. 3), an observation that supports my suggestion. Thus, in agreement with recent interpretations by Reid and Holl (2013), my findings indicate that trees will most likely act as nuclei when they facilitate seedling establishment and promote seed deposition.

This study shows that *F. natalensis* is an efficient nucleus during the nucleation process in miombo woodlands because it promotes seed deposition of animal-dispersed forest species and facilitates seedling establishment. However, the presence of *F. natalensis* may have negative effects on some other demographic stages. For example, seed predation is generally high under crowns compared to open microsites because rodents prefer to forage under trees where they experience lower predation risk (Smit et al., 2008). Thus, it is important to examine all demographic stages of recruitment, from seed arrival to seedling survival and growth, to fully evaluate the role of nuclei trees.

5 Conclusions

This is one of the very few studies to separately evaluate the importance of the perch and facilitative effects on the nucleation process. It was found that the perch effect increased seed deposition by frugivorous birds, and was a prerequisite for forest nucleation in areas of open vegetation. Furthermore, I demonstrated that the amelioration of microhabitat conditions in the vicinity of trees also significantly affects the dynamics of the nucleation process. Thus, the study suggests that trees drive the nucleation process when they promote seed deposition and have positive effects on the post-dispersal stages of plant recruits.

Acknowledgments

G. Yamakoshi, K. Zamma, S. Ichino, K. Mizuno and two anonymous reviewers are acknowledged for their constructive criticism of earlier drafts of this manuscript. This study enjoyed logistic support from the Forestry Research Institute of Malawi and

the National Herbarium and Botanical Gardens of Malawi. I would like to thank T. Chanyenga for his kind support and H. Patel for identification of plant specimens. This research was funded by the Japan Societyfor the Promotion of Science Global COE Programme (E-04): In Search of a Sustainable Humanosphere in Asia and Africa.

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